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Pairs of extreme avian personalities have highest reproductive success

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Summary

1. Intraspecific variation in reproductive decisions is generally considered as a reaction to environmental circumstances. We show that variation in reproductive parameters also covaries with intraspecific variation in personality.

2. During 4 years, we studied reproductive parameters in a natural population of great tits in association with a personality trait: exploratory behaviour as measured in a novel environment.

3. Nest success, fledgling size and condition were all correlated with this personality trait. Slow-exploring females had a higher nest success and largest fledglings. Fledgling condition was affected by the interaction between male and female exploratory behaviour, with assortative pairs at both ends of the behavioural spectrum producing fledglings in best condition. Fast-exploring males bred in nestboxes that produced heavy fledglings in other years.

4. We hypothesize that fast-exploring individuals are better able in defending or obtaining a high quality territory, while slow-exploring individuals are either better parents or have better chicks which may, in part, explain the patterns in reproductive success. We discuss how these patterns in reproduction can explain earlier reported relationships between offspring recruitment and avian personality and may result in the maintenance of intraspecific genetic variation in personality.

Key-words: boldness, exploration, fitness, genetic variation, personality, reproduction

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Introduction

Individual organisms react continuously to their environment in order to maximize their fitness but interestingly, even individuals of the same species differ in their behavioural reaction to the same environmental stimuli. This variation in behaviour is often not simply noise around a certain optimal strategy, but is highly repeatable within individuals (Clark & Ehlinger 1987; Wilson *et al.* 1994; Gosling 2001). Reactions to different environmental stimuli are furthermore often structured in correlated responses (Boissy 1995; Koolhaas, de Boer & Bohus 1997; Sih *et al.* 2004; Sih, Bell & Johnson 2004). These correlated responses are similar to variation in human personality (Wilson *et al.* 1994; Gosling & John 1999) and as in humans (Kagan, Reznick & Snidman 1988; Bouchard & Loehlin 2001), this personality variation normally has a genetic background (Bakker 1986; Henderson 1986; Benus *et al.* 1991; Sluyter *et al.* 1995; Weiss, King & Figueredo 2000; Drent, van Oers & van Noordwijk 2003). The existence of heritable variation in personality traits poses the question how natural selection acts on personality traits and how these alternative phenotypes can coexist (Wilson 1998; Dall, Houston & McNamara 2004), but so far fitness consequences have rarely been reported (Wilson *et al.* 1994; Armitage & Van Vuren 2003; Réale & Festa-Bianchet 2003; Dingemanse *et al.* 2004).

The variation we focus on is how individuals of a small songbird, the great tit *Parus major*, explore new

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environments (Verbeek, Drent & Wiepkema 1994). Earlier work on hand-raised great tits taken from a natural population showed that individuals differed consistently in their exploratory behaviour (Verbeek *et al*. 1994), and that exploration was correlated with aggressiveness (Verbeek, Boon & Drent 1996; Drent & Marchetti 1999), competitive ability (Verbeek *et al*. 1999), and social learning (Marchetti & Drent 2000). Two-way artificial selection and reciprocal crossing experiments showed that avian personality is highly heritable and that components of great tit personality are genetically correlated (van Oers *et al*. 2004). Recently we developed a laboratory test to measure the exploratory behaviour of free-living individuals (Dingemanse *et al*. 2002), which allowed us to examine the fitness consequences of this heritable trait in a natural population. This behavioural test is repeatable and parent-offspring regression yielded a heritability of 0·34 (Dingemanse *et al*. 2002; Dingemanse *et al*. 2004). Variation in exploratory behaviour was unrelated to sex, condition or raising conditions, and we regard this variation as different strategies in how individuals cope with challenges in their environment (Verbeek *et al*. 1994; Verbeek *et al*. 1996), comparable with variation in personalities (Dingemanse *et al*. 2002; Drent *et al*. 2003).

Fast-exploring and aggressive phenotypes are normally considered to have an advantage over slow-exploring and more docile phenotypes (Krebs 1978), and the naive prediction would be that these genotypes would increase in the population. Slow-exploring great tits, however, are found to be more sensitive to changes in their environment (Verbeek *et al*. 1994; Drent & Marchetti 1999) and are better able to cope with social stress (Verbeek *et al*. 1999; Carere *et al*. 2001; Carere *et al*. 2003). Exploration as measured in this study is thus not simply a measure of boldness in exploration, but predicts an individual's reaction towards a wide range of novel or challenging situations. Therefore, slow individuals may have a higher fitness than fast-exploring individuals under certain ecological circumstances and social environments. Recently we showed that exploratory behaviour affected dispersal (Dingemanse *et al*. 2003) and the ability to monopolize clumped food in the wild (Dingemanse & de Goede 2004), and that the survival consequences of avian personality varied between years in interaction with gender (Dingemanse *et al*. 2004). The number of offspring produced by these great tits that survived and recruited in the breeding population also related to their exploratory behaviour and selection again varied between years: in a rich year with high recruitment rates there was disruptive selection, with pairs of either two extremely slow or two extremely fast parents producing most recruits. In two poor years with low recruitment rates intermediate parents produced most recruits. These correlations between numbers of recruiting offspring and exploratory behaviour can have their origin in either different reproductive success and/or differences in survival of offspring during the non-reproductive period.

In this paper we examine the correlations between exploratory behaviour and reproductive parameters in four different years in a natural population of great tits to understand better when and how selection operates on avian personality. Knowledge about how selection on avian personality acts at different life-stages is essential to understand and predict how personality traits evolve and coexist in species that live in temporally changing environments. We realize that we can present correlations only between fitness measures and personality traits, but until now we could not manipulate personalities or pair composition experimentally in a natural population. Although the personality traits could in principle be affected by ontogenetic effects, cross-fostering experiments have failed to show that this is the case (Drent *et al*. 2003), and our field data thus most probably show how selection acts on genetic variation.

Methods

STUDY AREA AND FIELD METHODOLOGY

Data were collected in a nestbox breeding population of great tits in the southern Veluwe Area (study areas Westerheide and Warnsborn-West near Arnhem, the Netherlands, 5°50′E, 52°00′N) from 1999 to 2002. The study area consisted of a mixed pine–deciduous wood of 250 ha with about 600 nestboxes (for further details see Dingemanse *et al*. 2002). Nestboxes were checked twice a week from the beginning of April until the end of June. During the study period second broods (laid after a successful first brood) were rare and unsuccessful, and we therefore restricted the analyses to first broods only. Laying date is the date the first egg was laid, and clutch size is the number of eggs incubated. At the time the eggs were expected to hatch, nests were checked daily to record the day at which the eggs started to hatch (day 0). At day 7 the parents were caught in the nestbox using a spring trap, and the chicks were banded with uniquely numbered aluminium rings. Parents not banded as nestlings were aged as either 1 year old or older based on the colour of their greater coverts (Jenni & Winkler 1994). At day 14, when chicks have reached their fledging mass and size, we measured fledging mass to the nearest 0·1 g and fledging tarsus length to the nearest 0·1 mm. Tarsus length is considered to be a structural measure reflecting the skeletal size, and is referred to as fledgling size. We used fledgling mass at day 14 as a measure of chick condition by including fledgling size as covariate in the analyses (Keller & van Noordwijk 1993). At day 14 chicks were sexed on the basis of the colour of the greater coverts or using molecular markers (Griffiths *et al*. 1998). In 1999 37 of 59 broods were sexed molecularly, and we cross-checked our sexing in the field with the molecular sexing, which showed that field estimates had an accuracy of 82%.

To measure exploratory behaviour we captured individuals in the field outside the breeding season using

mist nets or roosting inspections, and transported them to the laboratory (Dingemanse *et al*. 2002). The birds always stayed for 1 night in the laboratory in individual cages (0·9 m × 0·4 m × 0·5 m) prior to testing. Individuals were tested alone during the morning following capture in a sealed room (4·0 m × 2·4 m × 2·3 m) with five artificial trees, and entered the room through a sliding door without handling. The exploration score used here is the number of movements (hops between branches within trees and flights among trees or other perches) during the first 2 min after the individual entered the room, corrected for date of capture based on within-individual changes in behaviour with capture date (Dingemanse *et al*. 2002). Fast explorers have higher exploration scores than slow explorers. Exploration scores were analysed using the raw scores and not on the categories 'fast' or 'slow', but for presentation reasons only we refer frequently to fast or slow.

STATISTICAL ANALYSES

All analyses were performed on mean values per nest and we included only those nests of which both parents were behaviourally tested. Sample sizes differed between analyses because in some years experiments were carried out in part of the area, and for some nests laying dates and clutch sizes were available but not the nest success or growth of the nestlings. In all analyses we tested the effects of year (factor with four levels), female age (factor with two levels distinguishing 1-year-olds from older individuals), male age (factor with two levels) and both female and male exploration score (covariates). We tested the quadratic effects of exploratory behaviour because we do not have a priori reasons to expect linear relationships. None of the quadratic effects were significant and they are not mentioned in the Results. In the analyses of clutch size, nest success, fledging size and fledging condition we also included laying date in the analysis to account for seasonal effects on these reproductive parameters (Verhulst, van Balen & Tinbergen 1995). Fledgling size depends not only on the environmental conditions during growth but also has a high heritable component (van Noordwijk, Balen & Scharloo 1988), mid-offspring – mid-parent h^2 in this study is 0·44, $P < 0·001$, $n = 150$ nests. To account for this heritable component we included the average tarsus length of the two parents as a covariate in the models on fledgling size.

All analyses were performed using general linear models (GLM). In case of binomial data we used logistic models, in all other cases we assumed a normal distribution. We tested all two-way interactions between explanatory variables. Because we carried out tests on, at most, 20 interactions per analysis (depending on the dependent variable), we include only the interaction terms for which the values of P were equal to or smaller than 0·01. In the results we show only those interaction terms that were significant on the basis of this criterion.

If individuals survived to the next year and bred again, they occurred more than once in the analysis. Although there is some pseudoreplication in case of multiple nests of the same individuals, the interaction between male and female exploration was significant in some analyses, which implies that the pair can be regarded as the independent unit of analysis. In 25 of the 225 cases male and female were the same in more than one year, but excluding these did not change the results. Excluding all multiple records of the same individual would have solved the problem of pseudoreplication, but with the cost of not being able to analyse age effects. In our opinion, the reduction of the data set to single records per individual is also arbitrary in the choice of records and therefore we chose to use all nests for which the exploratory behaviour of both pair members was known. This resulted in data sets in which between 72% and 82% of the records belonged to different individuals.

Correlations between exploratory behaviour and reproductive parameters can be explained either by variation in habitat quality, parental traits of males and females separately, and by interactions between these parameters. We estimated habitat quality on the basis of occupation and mean reproductive traits of the nestbox during the years 1995–2002. With this aim we calculated for each brood during the period 1995–2002 the deviation of laying date, clutch size, fledgling number, fledgling tarsus length and fledgling mass to the annual mean. Next we averaged these relative reproductive parameters for the focal nestbox over all years, excluding all nests in which one of the pair members of interest was involved. To avoid pseudoreplication in this measure of nestbox quality we only included the first nest of a female if she bred multiple times in the same nestbox. To estimate mean fledgling condition of the nestbox we only used the nestbox-specific relative fledgling mass because sample sizes for tarsus length were low. Because of sample size limits, in this analysis only we did not control for parental tarsus length when testing the effect of fledgling size, and here fledgling size was defined as the fledgling tarsus length of each nestbox. These measures indicated whether a nestbox was relatively early or late, and productive or not. We only used these relative nestbox values if these were based on at least two broods (sample sizes differ depending on the number of measurements of different reproductive parameters). We performed GLMs with these nestbox-specific estimates of territory quality as dependent variables and male and female exploratory behaviour and their interaction as explanatory variables.

Results

REPRODUCTION AND EXPLORATORY BEHAVIOUR

Laying date was unrelated to female ($F_{1,210} = 0·02$, $P = 0·89$) or male ($F_{1,211} = 0·10$, $P = 0·75$) exploratory

Table 1. The effect of exploratory behaviour of males and females on fledgling size and condition in a natural population of great tits. The results of GLM analyses are given for the mean tarsus length per nest (fledgling size) and the mean fledgling body mass (fledgling condition). Data were collected in 4 years, and ages of the parents were divided into first year and older. In the analysis of fledgling size we include the mean tarsus length of both parents as an approximation of the genetic effect. In the analysis of fledgling condition we include the mean tarsus length of the brood to control for the variation in size. If we do not include fledgling tarsus the analysis of fledgling mass is qualitatively similar

	Fledgling size			Fledgling condition		
	F	d.f.	*P*	*F*	d.f.	*P*
Year	11·42	3,142	0·000	NA		
Female age	NA			0·13	1,134	0·72
Male age	1·14	1,139	0·29	NA		
Female exploration	NA			NA		
Male exploration	3·11	1,140	0·080	NA		
Laying date	3·94	1,142	0·049	NA		
Parental tarsus	34·85	1,142	0·000			
Female age × female exploration	6·74	1,142	0·010			
Juvenile tarsus				NA		
Year × male age				4·98	3,135	0·003
Laying date × fledgling tarsus				10·64	1,135	0·001
Female × male exploration				7·82	1,135	0·006

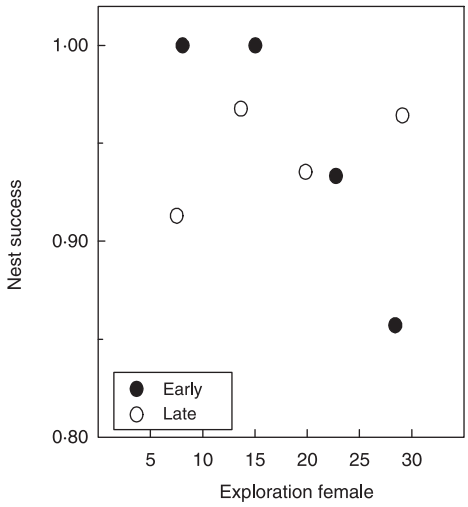

Fig. 1. The effect of female exploratory behaviour and laying date on the probability to fledge at least one chick in wild great tits. For graphical purposes we give the average probability per 25% category for female exploratory behaviour and for each female category we give the lower (solid) and upper (open dots) 50% of the laying date distribution. (year $\chi^2 = 15{\cdot}4$, $P = 0{\cdot}002$, interaction female exploration × laying date $\chi^2 = 8{\cdot}16$, d.f. = 1, $P = 0{\cdot}004$).

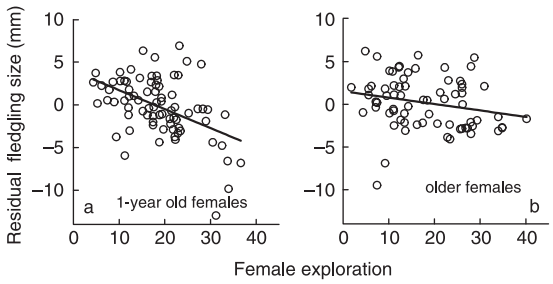

Fig. 2. The effect of female exploratory behaviour and age on mean fledgling size of their broods. For presentational purposes fledgling size is expressed as the residual of tarsus length on year, laying date, female age and parental tarsus length (see Table 1).

behaviour, and differed between years ($F_{1,212} = 33{\cdot}5$, $P < 0{\cdot}001$) and female age-classes ($F_{1,212} = 9{\cdot}23$, $P = 0{\cdot}003$). First-year females laid on average 2·5 days later than older females. Also clutch size was unrelated to either the exploratory behaviour of females ($F_{1,209} = 0{\cdot}08$, $P = 0{\cdot}78$) or males ($F_{1,207} = 1{\cdot}85$, $P = 0{\cdot}18$), and again varied between categories of year ($F_{3,210} = 17{\cdot}7$, $P < 0{\cdot}001$) and female age ($F_{1,210} = 4{\cdot}89$, $P = 0{\cdot}03$).

The probability of fledging at least one chick correlated with female exploratory behaviour in interaction with laying date (Fig. 1). For early nests slow-exploring females had the highest probability of fledging at least one offspring, whereas later in the season this effect disappeared (Fig. 1). For nests that fledged at least one offspring, the number of fledglings did not correlate with either female ($F_{1,152} = 0{\cdot}01$, $P = 0{\cdot}98$) or male ($F_{1,156} = 1{\cdot}23$, $P = 0{\cdot}27$) exploratory behaviour.

Fledgling size correlated negatively with female exploratory behaviour, but not with male exploratory behaviour, with the effect being stronger in young than in older females (Table 1, Fig. 2). This effect may have been caused by unequal brood sex ratios with respect to female exploratory behaviour, because male offspring have larger tarsi than female offspring. Inclusion of the observed sex ratio in the model showed that broods with more males indeed had longer tarsi ($F_{1,139} = 7{\cdot}02$, $P = 0{\cdot}009$), but the variance explained by female exploratory behaviour increased when sex ratio was added to the model (interaction female exploration × female age: $F_{1,139} = 9{\cdot}33$, $P = 0{\cdot}003$), showing that slow-exploring females indeed had fledglings that were larger in size.

Fledgling condition was affected by the interaction between male and female exploratory behaviour, with slow–slow and fast–fast pairs having chicks in the best

Table 2. Regression results of nestbox-specific reproductive parameters ('nestbox quality') and the exploratory behaviour of its occupants. Each row is a different multiple regression analysis, with the dependent variable in the row and the explanatory variables in the columns. The reproductive parameters of nestboxes were based on nests in which neither of the pair members was involved, and are only included if we had at least two records available for the nestbox from different years from different parents. All measures are standardized with respect to the annual mean. Productivity is the number of fledglings

	Female behaviour			Male behaviour			Female × male behaviour		
	F	d.f.	*P*	*F*	d.f.	*P*	*F*	d.f.	*P*
Laying date	2·01	1,168	0·16	0·32	1,167	0·57	1·55	1,166	0·21
Clutch size	0·33	1,137	0·57	0·02	1,136	0·90	0·87	1,135	0·42
Productivity	2·85	1,114	0·09	0·63	1,113	0·43	0·71	1,112	0·40
Fledgling size	1·11	1,40	0·30	0·01	1,39	0·94	0·89	1,38	0·35
Fledgling condition	0·31	1,59	0·58	5·59	1,60	0·02	0·00	1,58	1·00

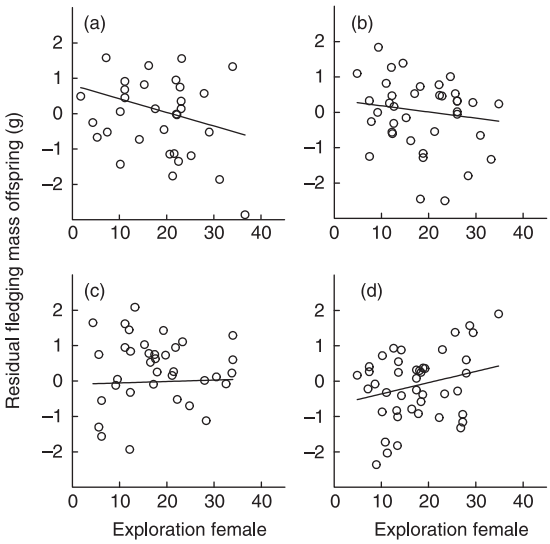

Fig. 3. Mean fledging condition per nest of juvenile great tits in relation to the exploratory behaviour of both parents. (a) males in the lowest 25%; (b) males having scores in 26th–50th percentile; (c) males having scores in 51st–75th percentile; (d) males in the highest 25%. Each graph represents fledgling condition across female mate exploration for each group of males. Analysis is performed on the raw exploration scores for males and females. For presentation purposes the fledging condition is expressed as the residual of fledging mass on year, male age, laying date, offspring tarsus length and the interactions between year × male age and laying date × tarsus (see Table 1). Lines are the regression lines for the model with the mean male exploratory behaviour of each quartile included.

condition (Table 1, Fig. 3). Fledgling condition was also affected by laying date of the clutch in interaction with the size, with chicks having lower condition for their size when born later in the season. In the first and third years, young males had fledglings in lower condition than older males, while the pattern was reversed in the other two years.

TERRITORY QUALITY AND EXPLORATORY BEHAVIOUR

The nestbox occupancy rate did not correlate with either female (GLM with binomial errors: $\chi^2 = 0{\cdot}08$, d.f. = 1, $P = 0{\cdot}78$) or male exploratory behaviour ($\chi^2 = 0{\cdot}74$, d.f. = 1, $P = 0{\cdot}39$), or their interaction ($\chi^2 = 0{\cdot}95$, d.f. = 1, $P = 0{\cdot}33$). We found no correlation between nestbox-specific laying dates, clutch sizes or productivity and exploratory behaviour of either parent occupying the box (Table 2). No correlation was found between exploratory behaviour of either pair-member and the average size of the fledglings of the occupied nestbox produced by other birds in other years, but fast-exploring males occupied nestboxes in which young fledged at a higher than average condition (Table 2). Nest boxes did not differ in exploratory behaviour of either the male (repeatability = −0·09, $F_{35,46} = 0{\cdot}81$, $P = 0{\cdot}74$) or female inhabitant (repeatability = −0·08, $F_{39,47} = 0{\cdot}83$, $P = 0{\cdot}73$, only nestboxes included with at least two values for either male or female exploratory behaviour), and hence the correlations between nestbox quality and exploratory behaviour did not originate from certain personalities nesting more frequently in certain nestboxes. These analyses suggest that fast-exploring males occupy nestboxes of better quality.

Discussion

The coexistence of different heritable behavioural strategies can be understood only if we have good fitness measures and understand the selection pressures causing these patterns in fitness. In an earlier study we showed that exploratory behaviour in this small songbird correlated strongly with fitness components for both adult survival and the annual number of recruiting offspring (Dingemanse *et al.* 2004). In one year both pairs of either two slow-exploring or two fast-exploring individuals produced most recruiting offspring (Dingemanse *et al.* 2004). Here we show that one of the underlying causes of these fitness patterns is that these pair combinations produced fledglings in the best condition. Furthermore, slow-exploring females had the highest probability of fledging at least one chick, fledglings of slow-exploring females were larger in size and fast-exploring males bred in nestboxes that produced heavy fledglings when occupied by other birds.

We showed that several reproductive traits are correlated with the personality of individuals or pairs. To

estimate overall fitness consequences of personality, we need to integrate these components to an overall measure of the genetic contribution of each individual/pair to the next generation. We conducted this recently by examining both the number of young that recruited in the local breeding population and the annual survival of the adults (Dingemanse *et al*. 2004). Here we focus on the underlying causes of the effects of personality on number of offspring surviving to breed in the local study area (recruits), because variation in recruitment may have its cause in the nestling period. In one of three years we found that assortatively mated pairs at both ends of the behavioural spectrum produced most recruits in the local study area, while in two other years birds of intermediate exploratory behaviour produced most recruits (Dingemanse *et al*. 2004). Because the probability of becoming a recruit depends to a large extent on condition at fledging (Tinbergen & Boerlijst 1990; Both, Visser, & Verboven 1999), the effect reported here that slow–slow and fast–fast exploring pairs have fledglings in the best condition can explain this pattern in recruitment rate in this one year, but not in the other two years. The single year when the fledgling condition and recruitment patterns matched was the year with high juvenile survival rates because of a good food stock in the winter (mass seeding of European beech *Fagus sylvatica*) and low adult population density and hence low competition for winter food and territorial space. Selection in that year may have operated on physical characteristics instead of behavioural characteristics of the juveniles. In the other two years there was little food in winter and a relatively high adult population density resulting in low juvenile survival rates, and under these circumstances selection on physical differences may be less important than selection on behavioural traits. This may explain that we found a tendency for stabilizing selection in these years on exploratory behaviour (Dingemanse *et al*. 2004) despite the fact that chicks from pairs at both extremes of the behavioural spectrum were in the best condition at fledging (this study).

One of the important findings is that offspring condition did not depend solely on the personality of each parent separately, but also on the interaction between male and female personality, with slow–slow and fast–fast pairs producing offspring in best condition. Because fledgling condition is an important determinant of fitness (Tinbergen & Boerlijst 1990; Both *et al*. 1999) one would expect selection to favour assortative mating with respect to exploratory behaviour, because this will enhance fitness for at least the birds at the opposite ends of the behavioural spectrum. Interestingly, there is disassortative mating for older, but not for 1-year old individuals (Dingemanse *et al*. 2004). Although we do not expect disassortative mating based on the data presented in this paper, we suggested that medium-exploring birds had the highest survival and offspring recruitment in the long term, because of the changing survival selection across years and sexes and the multiplicative nature of fitness (Dingemanse *et al*. 2004). Alternatively, fast-exploring males with their high quality territories could attract slow females that are more successful in nesting and have larger offspring, and this mating pattern could also result in disassortative breeding pairs. If this were true, then we expect fast male-slow female pairs to have the largest number of recruits, with natural selection favouring the evolution of sex-specific differences in personality. Neither of these results was found. Thus, although assortative pairs had chicks of highest condition and most recruits in some years, selection over the entire life span may nevertheless favour disassortative mating, because this apparently allows birds at the extremes of the behavioural distribution to increase their fitness by producing medium-exploring offspring.

The correlation between reproduction and exploratory behaviour may have been caused by variation in parental traits, territory quality, or both (Both & Visser 2000). Covariation between offspring condition and parental personality is likely to be mediated in part via territory quality, because fast-exploring males occupied better quality territories and fast–fast pairs produced offspring in best condition. This is consistent with the observation that fast-exploring territorial males outcompete slow-exploring territorial males at clumped food sources in winter (Dingemanse & de Goede 2004), and these fast-exploring males can thus be expected to acquire territories with the best foraging habitats. Although this could explain why some fast-exploring males had offspring of high condition, it does not account for the effect that slow-exploring pairs also had offspring fledging in high condition. The trait that may make slow-exploring individuals better parents is that slow birds are well adapted to forage under changing feeding conditions because they respond more quickly to changes in food distribution and explore alternative feeding options continuously (Verbeek *et al*. 1994; Drent & Marchetti 1999). Such foraging behaviour may be particularly beneficial during chick feeding, because great tits feed their offspring with mobile and hidden invertebrate prey and their foraging strategy may compensate for the lower quality of territories occupied by slow-exploring males. If slow-exploring mothers are indeed better adapted to provide nestling care, this may also explain why they had fewer nest failures and produced larger fledglings. This was especially true for what can be considered as unfavourable conditions: breeding early in the season may require more energy and hence slow exploring females did especially well in this period. That inexperienced slow females had larger fledglings than fast explorers can also be explained by their better ability to react to novel circumstances. Thus both variation in habitat and parental behaviour – resulting from differences in aggressiveness and foraging strategies – may explain why offspring condition covaried with parental personality.

The effect of pair composition on offspring condition indicates that certain personality types do not form good teams: fast-exploring males had high quality territories

but nevertheless produced offspring of low fledging condition when they had a slow-exploring mate. Similarly, slow-exploring males had low quality territories but can still produce offspring of high fledging condition if they had a slow-exploring mate. This effect of pair combination may be explained by better co-operation of individuals of similar personalities during the breeding season, but may also have its origin in how personality of chicks affects sibling competition and/or communication between parents and offspring (Carere 2003).

Spatial variation in territory quality and differential effects of territory quality on reproductive success may result in frequency dependent selection on variation in personality. We showed that fast-exploring males monopolized the best quality territories, but that slow-exploring males were nevertheless able to gain high reproductive success on their low quality territories. If fast explorers are rare, they may occupy the best territories, and their reproductive success being on average higher than that of slow explorers. In contrast, if fast explorers are common, their average territory quality will be lower resulting in low reproductive success, which may be lower than the rare slow explorers that are also in low quality territories but that have higher reproductive success. Such a frequency-dependent reproductive success may work if the reproductive success of slow explorers is less sensitive to territory quality, than of fast explorers. Frequency-dependent selection resulting from spatial variation in territory quality and different competitive and parental capacities may allow for the coexistence of this genetic variation in personalities in natural populations, especially if it works in concert with the earlier reported temporal variation in selection pressures (Dingemanse *et al*. 2004).

We have shown that intraspecific variation in reproductive success is not just the result of (noise around) a general reaction to the environment that is equal for each individual bird. Instead, individuals with different personalities have different reproductive output that in turn affects components of fitness. Variation in reproductive success can partly explain why pairs differ in the number of offspring that survive to become breeders, but selection acting on behavioural traits of offspring outside the breeding season appeared to be most important in years when few offspring survive.

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